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INFLUENCE OF FOREST EDGE ON NEST-SITE SELECTION BY TREE SWALLOWS

WALLACE B. RENDELL AND RALEIGH J. ROBERTSON[1]

ABSTRACT.—We examined the influence of forest edge on nest-site selection by Tree Swallows (*Tachycineta bicolor*) at nest-box grids in uniform habitats. Tree Swallows occupied nest sites at distances of 3–100 m from forest edge, while House Wrens (*Troglodytes aedon*) and most Eastern Bluebirds (*Sialia sialis*) used boxes within 30 m of forest edge. Mean distance to forest edge for the distribution of nest boxes used by Tree Swallows was greater than those means for Eastern Bluebirds and House Wrens, but mean distances to forest edge for nest boxes occupied by the latter two species were not different. Partial correlation analysis showed that settlement dates at nest boxes by single Tree Swallows (often known to be males), and dates of pair formation, were correlated negatively with distance to forest edge (i.e., Tree Swallows settled first at nest boxes that were farthest from forest edge). Also, when a pair of Tree Swallows had a choice of more than one nest box in which to breed (i.e., their territory included more than one nest box), they selected most frequently the nest box farthest from forest edge. Whereas predation by raccoons (*Procyon lotor*) and black rat snakes (*Elaphe obsoleta*) at Tree Swallow nest boxes occurred at distances from forest edge up to 80 m, House Wrens destroyed eggs and usurped nest boxes from Tree Swallows only within 20 m of forest edge. Further, although Eastern Bluebirds did not usurp nest boxes from Tree Swallows, both species are known to compete aggressively for boxes. Therefore, Tree Swallows may select nest sites farther from forest edge to avoid the costs of aggression or nest destruction that may be incurred during interactions with competitors, especially House Wrens. *Received 8 Sept. 1989, accepted 20 Feb. 1990.*

Nest-site selection by secondary cavity-nesting birds is an important determinant of fitness because several characteristics of nest sites can influence reproductive success. For example, cavity height influences success since lower cavities are more susceptible to predation (Nilsson 1984, Rendell and Robertson 1989). Also, clutch size is positively influenced by cavity size for many species (Karlsson and Nilsson 1977, Rendell and Robertson 1989). Further, habitat cover and foliage density influence fledging success for House Wrens (*Troglodytes aedon*) which are better able to detect and deflect predators in sparsely foliated vegetation than in dense vegetation (Finch 1989).

In this study we examined the influence of distance to forest edge on nest-site selection by Tree Swallows (*Tachycineta bicolor*). Observations of settling patterns of Tree Swallows breeding in grids of nest boxes gave the general impression that early settling pairs avoided boxes near forest edge. Subsequently, boxes near forest edge were often occupied by House

[1] Dept. Biology, Queen's Univ., Kingston, Ontario K7L 3N6, Canada.

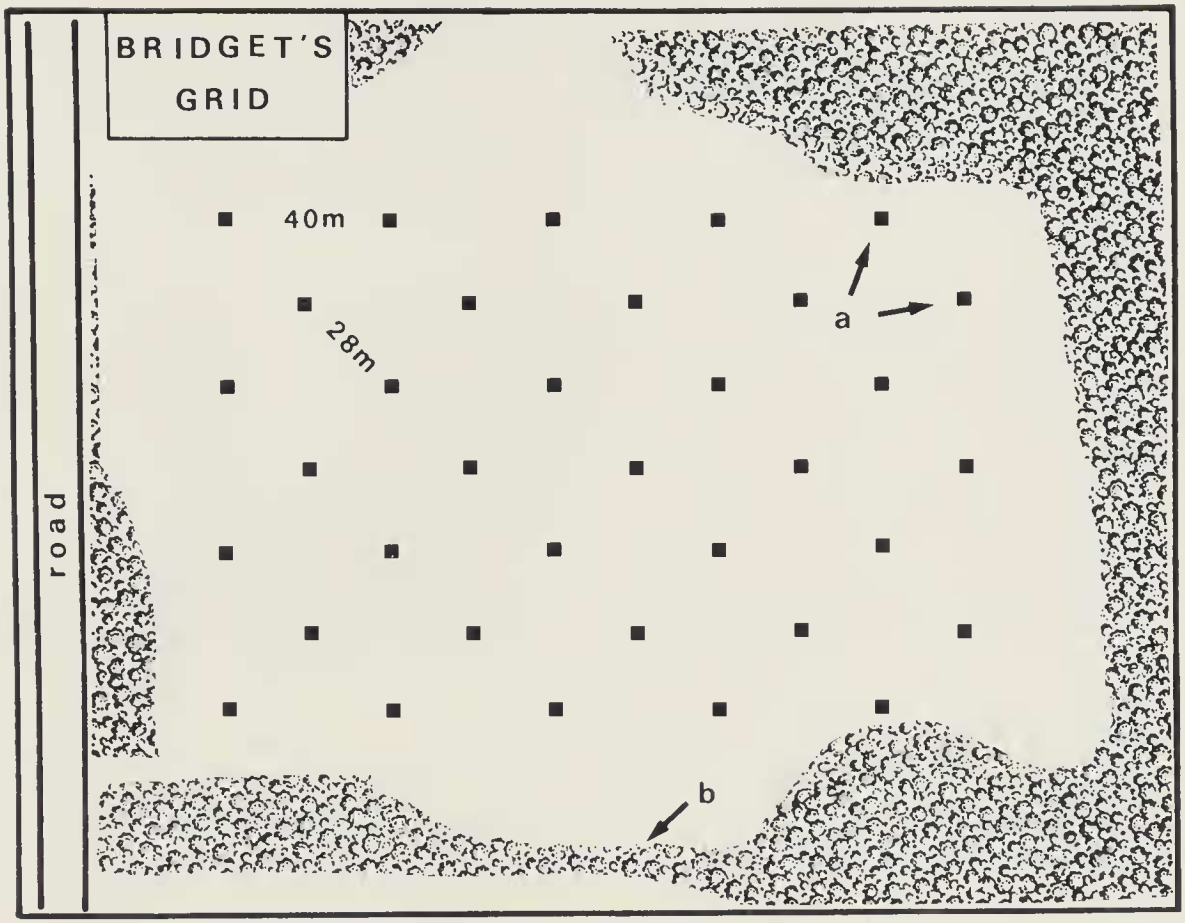


FIG. 1. Scale diagram of Bridget's Grid showing the arrangement of boxes in a grid, boxes at the grid edge (a), and forest edge (b).

Wrens and Eastern Bluebirds (*Sialia sialis*). Here we quantify those settling patterns and the distribution of nest failures caused by predation and nest-box usurpation and argue that Tree Swallows prefer to nest farther from forest edge to avoid interference from competing species, especially House Wrens.

STUDY AREA AND METHODS

Data were collected from 1986–1989. Three species (Tree Swallows, Eastern Bluebirds, and House Wrens) bred at grids of nest boxes located in four hayfields (Bridget's Grid [Fig. 1], BG; Hughson's Grid, HU; New Barn Grid, NB; and Sand Pit Grid, SP) on research tracts of the Queen's University Biological Station, Chaffey's Lock, Ontario. The hayfields ranged in size from 0.8–2.8 ha, and all four fields were situated within 0.8 km of each other. Three fields (BG, NB, and SP) were bordered on at least three sides by deciduous forest edge consisting primarily of poplar (*Populus* spp.), maple (*Acer* spp.) and oak (*Quercus* spp.). Hughson's Grid was bordered more distantly on two sides by forest and on two sides by field and marsh.

An abundant supply of nest sites (N = 77) was available at each grid in each year (BG, 35; HU, 18; NB, 14; and SP, 10), with additional nest sites available at three grids in 1986

only (BG, 3; NB, 1; and SP, 1). Nest boxes were mounted on aluminum poles (1.5–2.0 m high) arranged in columns and rows throughout each field; the distance between nearest boxes in a row or column was 40 m, and the distance along the diagonal was 28 m (Fig. 1). All nest-box entrances faced east, and all boxes and entrances were standard size (cavity volume = 3897 cm^3, entrance diameter = 3.7 cm), except in 1989 when the volume of boxes on alternate nest sites at BG was reduced by half (ca 1700 cm^3) as part of a separate study.

At alternate nest sites at HU (1987–1988) and BG (1987–1989), a second nest box was situated 8 m from the original box (i.e., boxes were paired), again as part of a separate study. We use the term nest site to refer to the physical cavity in which a pair nests (i.e., focal box), as well as the habitat surrounding a focal box. Since Tree Swallows usually defend territories with a radius of at least 10 m around a focal box (Robertson and Gibbs 1982, Muldal et al. 1985) we consider each of the sites with paired boxes as a single nest site because simultaneous use of the remaining box by another species or conspecific pair was precluded in most cases. Simultaneous occupancy of both of a pair of boxes either by different species or different breeding pairs occurred only 6 of 72 (8%) possible times. Thus, sample sizes indicate the number of nest sites available. Although most Tree Swallows defended only one nest site (either a single box or pair of boxes within 8 m) some initially defended larger territories which encompassed more than one nest site (i.e., single or paired boxes 28–40 m apart).

Surveys at all grids from late March to August throughout each breeding season enabled us to map which nest sites were used by a given species. A nest site was occupied when a species attempted to breed at the site (e.g., nest-building, egg laying, etc.), and also when a species actively prevented competitors from access to a box, either through territorial defense (e.g., Tree Swallows) and/or by nest-building (e.g., dummy nests of male House Wrens; cf, Finch 1989). The distances from the focal box in a territory to the nearest forest edge, and to the nearest grid edge (Fig. 1), were measured. Nest sites that were located along the periphery of a grid were defined as being on the grid edge, and therefore, the distance of a focal box on these nest sites to the grid edge was zero.

For Tree Swallows, settlement dates at nest sites at the two largest grids (BG and HU) were recorded by doing daily scans of the grids (cf, Stutchbury and Robertson 1987a) from the time of arrival of the first birds in late March or early April until most nest sites were occupied and nesting was underway in early May. In 1986, data were available for settlement dates of pairs, while in 1987–1989, settlement dates of both single individuals (often known to be males) and pairs were available.

RESULTS

Occupancy.—Tree Swallows occupied the vast majority of available nest sites at all grids during the study (N = 294; Fig. 2). House Wrens occupied 18 nest sites, mostly at BG and SP. House Wrens were common from 1986–1988, but only one pair nested at BG in 1989. House Wrens never bred at HU grid. Eastern Bluebirds also occupied nest sites at all grids in each year (N = 26). Nest-site occupancy rates were high in all years at each grid (range 93–100%), and all nest sites were used at some time during the study. Twenty-one nest sites were used twice (and were therefore considered to be available twice), and four nest sites were used three times (and were therefore available three times) in a given year,

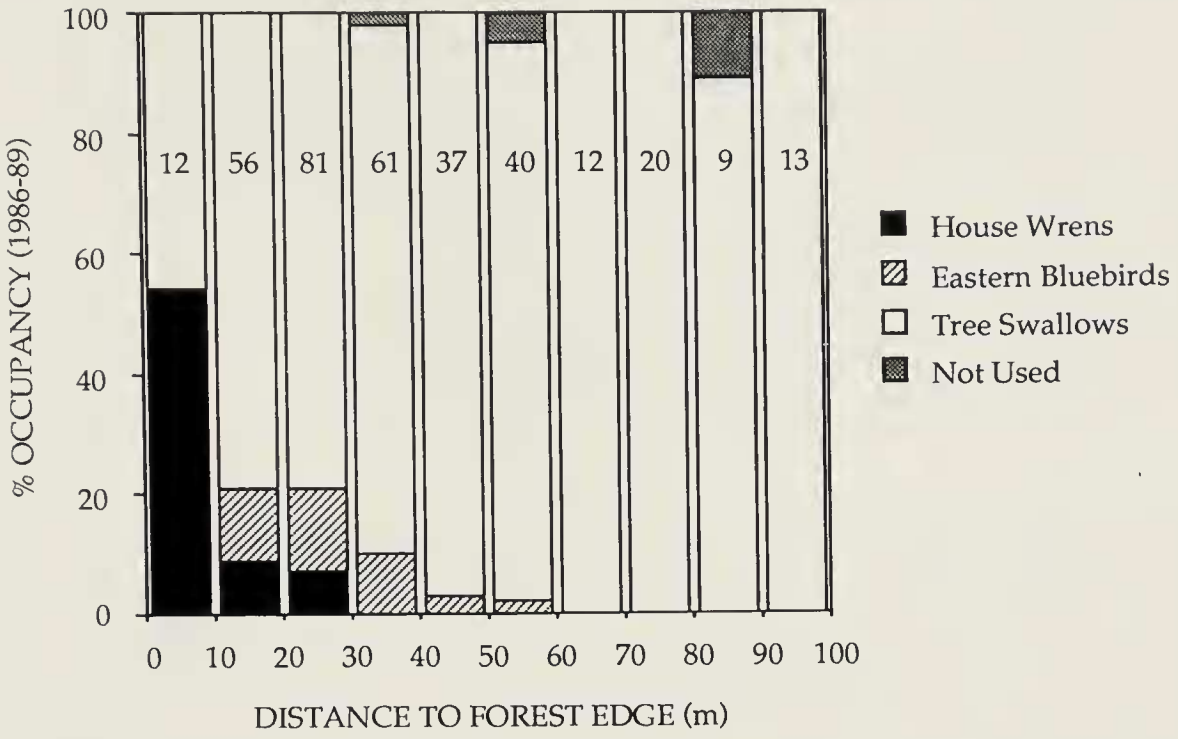
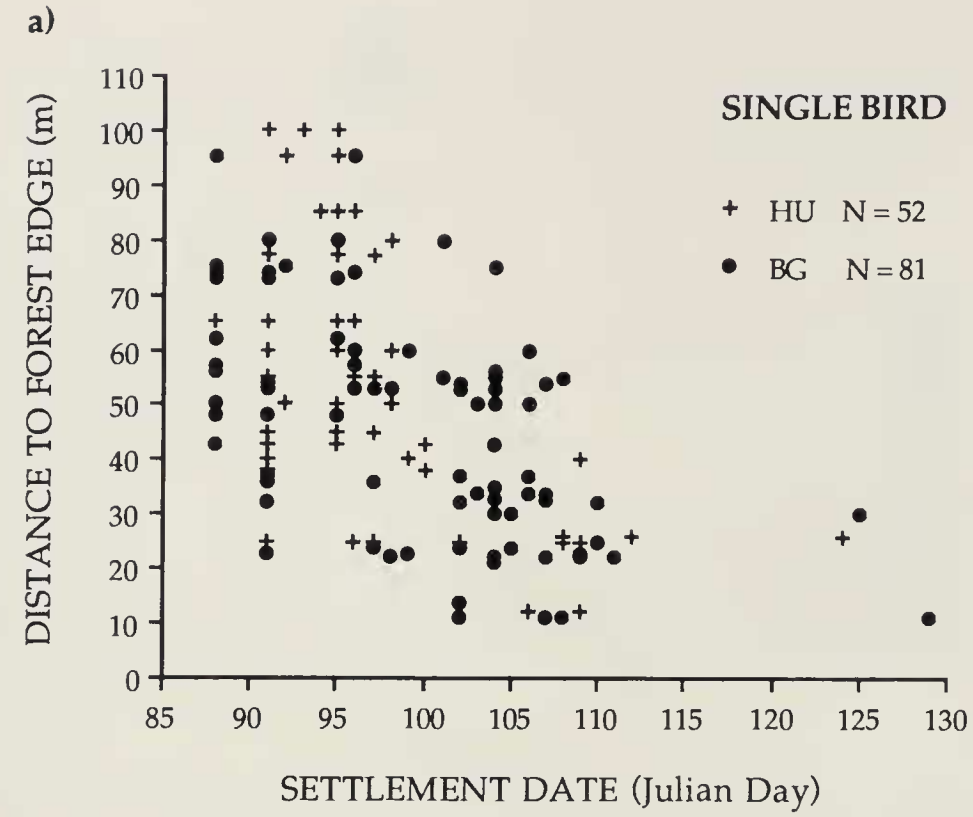


FIG. 2. Distribution of nest sites used by Tree Swallows, House Wrens, and Eastern Bluebirds, and those not used, relative to distance to forest edge (1986–1989). Sample sizes of the number of nest sites available for use are presented within each distance cell.

often by different species; hence, the total number of nest sites used by all three species combined (N = 338) was greater than the number of available nest sites throughout the study (N = 313).

House Wrens occupied nest boxes close to forest edge (range 3–30 m). Most Eastern Bluebird pairs (69%; 18/26) also nested less than 30 m from forest edge, but the range of distances from forest edge for this species (10–53 m) was greater than that for House Wrens. Tree Swallows occupied boxes at all distances from the surrounding edge (range 3–100 m), and only this species used boxes greater than 60 m from forest edge (Fig. 2). Mean distances to forest edge for distributions of nest boxes used by House Wrens ($\bar{x}$ = 13.9 ± 2.2 [SE] m, N = 18) and Eastern Bluebirds (25.8 ± 2.2 m, 26; Tukey HSD Multiple Comparison, $q_{[0.05]} = 2.55$, df = 335, $P > 0.05$) were not different. Mean distances to forest edge for nest boxes of House Wrens and Tree Swallows (41.3 ± 1.3 m, 294; Tukey HSD, $q = 7.40$, df = 335, $P < 0.05$), and Eastern Bluebirds and Tree Swallows (Tukey HSD, $q = 4.96$, df = 335, $P < 0.05$), were different.

Forest edge avoidance by Tree Swallows.—Settlement dates of Tree Swallows at nest sites in BG and HU from 1986–1989 were negatively correlated with distance to forest edge and distance to grid edge (Table 1). Nest sites farther from forest edge and grid edge were settled earlier


a)
SINGLE BIRD
+ HU N = 52
● BG N = 81
DISTANCE TO FOREST EDGE (m)
SETTLEMENT DATE (Julian Day)
0
10
20
30
40
50
60
70
80
90
100
110
85
90
95
100
105
110
115
120
125
130

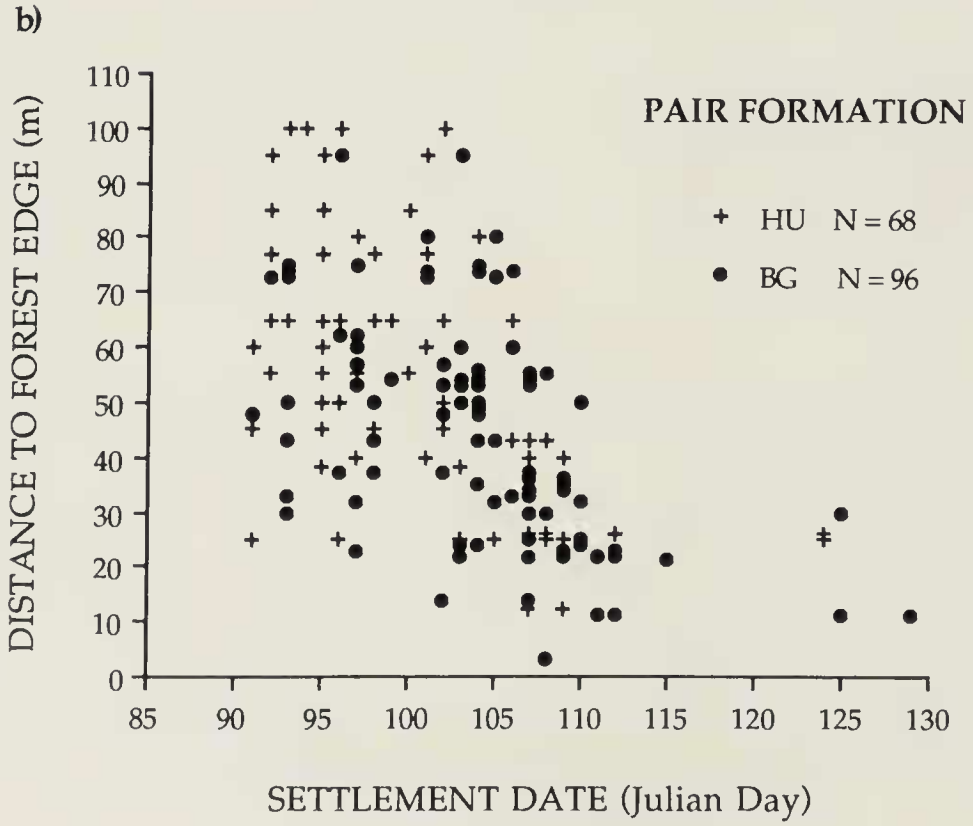

b)
PAIR FORMATION
+ HU N = 68
● BG N = 96
DISTANCE TO FOREST EDGE (m)
SETTLEMENT DATE (Julian Day)
0
10
20
30
40
50
60
70
80
90
100
110
85
90
95
100
105
110
115
120
125
130

TABLE 1

PEARSON CORRELATION COEFFICIENTS FOR SETTLEMENT DATES[a] OF TREE SWALLOWS WITH DISTANCE TO FOREST EDGE AND GRID EDGE AT BRIDGET'S GRID (BG) AND HUGHSON'S GRID (HU), 1986–1989

Grid	Years	Forest edge		Grid edge	
		One bird (N)	Pair (N)	One bird (N)	Pair (N)
BG	1986–1989	−0.538[b] (81)	−0.492[b] (96)	−0.469[b] (81)	−0.393[b] (96)
HU	1986–1989	−0.537[b] (52)	−0.548[b] (68)	−0.301[b] (52)	−0.263[b] (68)

[a] Julian day 91 = 1 April.
[b] Correlation coefficients are significant at $P \leq 0.05$.

by single birds and pair formation occurred earlier at these nest boxes in both grids. Distance to forest edge and to grid edge were significantly positively correlated with each other (at BG, 1986–1989, 0.82, $P < 0.01$; at HU, 1986–1989, 0.32, $P < 0.05$). Partial correlation analysis showed that nest-site settlement dates by Tree Swallows were negatively correlated with distance to forest edge at BG and HU (Fig. 3a, b), when controlling for distance to grid edge (Table 2). The alternative test (i.e., controlling for distance to forest edge) found no correlation of settlement date with distance to grid edge at either grid.

Early in the breeding season, many pairs of Tree Swallows initially defend territories that include more than one nest site (cf, Rendell and Robertson 1989). When a pair of Tree Swallows had a choice between nesting at one nest site or another, pairs chose most frequently to breed at the nest site farther from the forest edge. Tree Swallow pairs defended two or more nest sites on 44 occasions over four years (BG, 23; NB, 9; SP, 12). In 33 of these 44 cases, one or both nest sites were less than 30 m from forest edge (i.e., within the distance to edge where most House Wren and Eastern Bluebird pairs occupied nest sites; Fig. 2). In 25 of these 33 cases, Tree Swallows ultimately nested at the nest site farther from the forest edge (Binomial Test, $P = 0.002$). In these 25 cases, pairs were not forced to nest farther from edge as a result of losing a nest site to competitors but "chose" to breed at the nest sites farther from edge.

Predation and interference.—Predators preyed on nest contents, and House Wrens usurped focal nest boxes, at 43 of 299 (14.4%) breeding attempts (i.e., where at least one egg was laid) by Tree Swallows for all

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FIG. 3. Plots of settlement date (Julian day 91 = 1 April) at nest sites and distance to forest edge for Tree Swallows at Bridget's Grid and Hughson's Grid: (a) single birds, usually known to be males, 1987–1989, and (b) two birds (pair formation), 1986–1989.

TABLE 2
PARTIAL CORRELATIONS OF SETTLEMENT DATES AT BRIDGET'S GRID AND HUGHSON'S GRID, CONTROLLING FOR DISTANCE TO FOREST EDGE (FORED) AND GRID EDGE (GRDED), 1986–1989

Grid		Forest edge (controlling GRDED)		Grid edge (controlling FORED)	
		One bird (N)	Pair (N)	One bird (N)	Pair (N)
BG	settlement date	−0.304* (81)	−0.322* (96)	−0.066 (81)	0.024 (96)
HU	settlement date	−0.489* (52)	−0.507* (68)	−0.166 (52)	−0.110 (68)

* $P \leq 0.01$.

grids and years combined. The number of breeding attempts exceeds the number of nest sites occupied by Tree Swallows because several pairs renested in the same nest site in a given year (e.g., due to predation at first nest). Two terrestrial predators, raccoons (*Procyon lotor*) and black rat snakes (*Elaphe obsoleta*), were responsible for 62.8% (27/43) and 20.9% (9/43) of all acts of predation, respectively. House Wrens were responsible for the remaining 16.3% (7/43) of interference at Tree Swallow nests. House Wrens pecked eggs (cf, Belles-Isles and Picman 1986) and/or built their nests over active Tree Swallow nests. Predation by raccoons occurred only in 1987. Late in the breeding season of 1987, predator cones were installed at all boxes, effectively eliminating any threat of predation from terrestrial animals, but this did not prevent access to boxes by House Wrens. As a result, the following results describing predation by terrestrial animals are restricted to 1986–1987 only, while House Wren data from 1986–1989 are described.

From 1986–1987, 159 nest sites were available for use at all grids combined, and predation and/or interference occurred at 40 of these nest sites. The distribution of the number of nest sites where predation/interference occurred (presented as percentages in Fig. 4) relative to distance to forest edge did not differ from the distribution of nest sites where such events did not occur (Pearson chi-square, $\chi^2 = 2.67$, df = 5, $P = 0.75$). Therefore, predation and interference appears to have occurred at any nest site despite its proximity to forest edge. However, this analysis does not account for the different types of predators and competitors involved. Raccoons and black rat snakes were a threat to Tree Swallows at all distances from forest edge up to 80 m, but House Wrens interfered only at nests within 20 m of forest edge ($\bar{x} = 9.0 \pm 1.7$ m, range = 3.1–17.0 m, N = 7; including two acts of interference committed in 1988; Fig. 4). Clearly, the likelihood of a Tree Swallow nest being destroyed by House Wrens decreases as distance to forest edge increases.

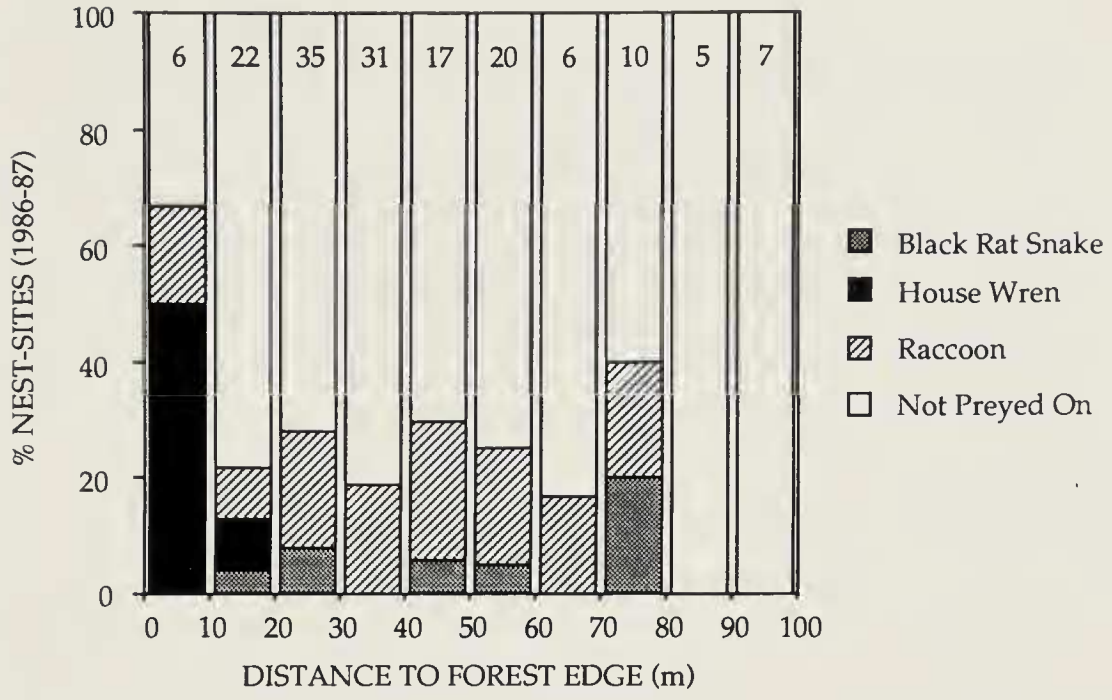

FIG. 4. Distribution of Tree Swallow nest sites that were usurped or where predation occurred, and those that were not influenced by predators or competitors, relative to distance to forest edge (1986–1987 for all predators and competitors). Sample sizes of the number of nest sites available for use are presented for each distance cell.

DISCUSSION

When Tree Swallows had a choice of nest sites on which to settle and breed, they avoided nesting close to forest edge. Single birds (assumed and often known to be early arriving males, Stutchbury and Robertson 1987a) settled at nest sites farther from forest edge first, and females subsequently settled first with males situated near the center of the population. Since Tree Swallows are limited by nest-site availability (Holroyd 1975, Stutchbury and Robertson 1987b, Rendell and Robertson 1989), rather than forego breeding, late-arriving birds were forced to use nest sites closer to forest edge. Apparently, both males and females selected nest sites based on the same criteria, consistent with the suggestion that characteristics of nest sites may act as cues to breeders concerning the likelihood of nesting success (Nilsson 1984, Finch 1989).

Our results appear to contradict Muldal et al. (1985) who studied spacing patterns of Tree Swallows in nest boxes arranged in spirals in the same fields as this study. One of their conclusions, that Tree Swallows settled at a spiral independently of its location in a field, was based on the assumption that settlement date is correlated with first egg date. Stutchbury and Robertson (1987a) have subsequently shown this not to be the case. Therefore, while their interpretation of patterns of actual nest-box

occupancy over short distances remains valid, the absence of direct information on settlement patterns prevented Muldal et al. (1985) from detecting preferences for nest sites in relation to location within a field.

Why should Tree Swallows avoid nesting close to forest edge? We suggest this behavior is a response to greater likelihood of interference by competing species, especially House Wrens, near forest edge. Similar to our study, Munro and Rounds (1985) found House Wrens typically nested within 30 m of forest edge, and Willner et al. (1983) found House Wrens nested in boxes closer to trees and shrubs than Tree Swallows, and that Eastern Bluebirds were intermediate to both species (see Fig. 2). Further, House Wrens commonly interfere with breeding attempts by Tree Swallows (Kendeigh 1941, D. M. Finch, pers. comm., this study), and Eastern Bluebirds, although not observed to usurp nest sites from Tree Swallows in this study, do compete aggressively for nest sites (Kuerzi 1941). Therefore, by selecting nest sites more distant from forest edge, Tree Swallows can avoid the costs of harassment or nest destruction which are incurred during competition with Eastern Bluebirds and House Wrens.

Tree Swallows may choose to nest farther from forest edge for other reasons as well. Tree Swallows are aerial insectivores that commonly forage over open fields and water. Nesting away from forest edge likely allows clear flight paths for foraging in the vicinity of the nest site. Also, some benefit may be derived from nesting centrally to other breeding pairs. For example, Tree Swallows respond to avian predators (e.g., Sharp-Shinned Hawk [*Accipiter striatus*]) by alarm-calling, mobbing, and chasing a threatening hawk. The characteristics of grid geometry (see Fig. 1; cf, Hamilton 1971, Wittenberger and Hunt 1985) may render birds nesting farther from forest edge, and/or centrally to other pairs, less susceptible to attacks from accipiters. Nesting centrally to other pairs may also reduce the likelihood of predation from terrestrial animals. However, our data on predation by raccoons and black rat snakes do not support this idea.

Many social and historical factors also play a role in nest-site selection. For example, the presence of a previous mate (R. R. Cohen, pers. comm.) or a history of successful nesting at a particular site (Pinkowski 1979, Sonerud 1985, Drilling and Thompson 1988) may influence where an individual Tree Swallow settles. In our study, all physical characteristics of nest sites (e.g., habitat structure, box height and orientation) were essentially uniform, except for distance to forest edge. Given the influence of social factors and past breeding experience on nest-site selection, it is remarkable that distance to forest edge apparently plays such an important role in determining nest-site selection and, hence, settling patterns of Tree Swallows.

Distance to forest edge is likely an important factor in nest-site selection

in natural habitats as well. In a study of Tree Swallows breeding at beaver ponds, Rendell and Robertson (1989) found nest cavities that were preyed on were considerably closer to shore (i.e., forest; $\bar{x} = 26.4 \pm 4.5$ m, N = 15) than those that fledged young (47.9 ± 9.2 m, 22), although this difference was not significant. Tree Swallows and other hole-nesters in these populations may increase their likelihood of reproductive success by choosing to occupy cavities as far from shore as possible upon returning each spring. Unfortunately, we do not have settlement data for Tree Swallows in natural populations.

In conclusion, when Tree Swallows had a choice of where to nest in a population, they chose nest sites farther away from forest edge. This behavior may be an adaptive response to a greater threat of competitive interference from other species for nest sites near forest edge. The addition of distance to forest edge to other characteristics of cavity nest sites that are known to influence reproductive success (i.e., cavity height, cavity volume) suggests that nest-site selection by secondary cavity-nesting birds is an important and complex decision involving many variables.

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